

Reciprocity: Cooperation based on repeated interactions

An individual X may profit from benefiting another individual Y if there is a high likelihood that Y will provide reciprocal aid in the future (Trivers 1971). The mathematical condition for helping to evolve is then

$$\omega m \beta B - C > 0$$

where ω is the probability that an individual will interact with the same partner again, m is the ability to remember the partner's previous cooperation, β is the individual's response to the partner's previous level of cooperation, and B is the total fitness benefit from helping (Lehmann and Keller 2006). The critical points are that there must be repeated interactions, individuals must recognize and remember each other, and the benefit must be great enough to outweigh the cost of helping.

This is a complex topic, because of the obvious possibility that Y will defect and X will have paid the cost without recompense. The conditions under which cooperation can evolve have been analyzed by game theory, especially analyses of the "prisoner's dilemma" (Axelrod and Hamilton 1981). This is named for the situation in which two imprisoned suspects could cooperate by agreeing not to give evidence against each other (cooperation that would benefit both), but each is rewarded by the police if he or she selfishly acts as informant. The simplest strategy is "tit for tat," in which each "player" starts with cooperation and then does whatever the other has done in the previous round. However, this strategy does not allow for accidental mistakes. Among various alternatives, a perhaps more stable strategy that maintains cooperation is one in which each individual repeats its previous move whenever it is doing well, and changes otherwise (Nowak 2006). Bear in mind that the term "strategy" does not imply conscious reasoning or planning; a strategy is simply a phenotypic character, such as a particular behavior, of a certain genotype.

Reciprocity of this kind, based on "partner choice," appears to be uncommon, perhaps because it requires rather complex information processing to distinguish different individuals and remember their past behavior (Hammerstein 2003). Reciprocity is obviously a major feature of human social systems, and has been shown for some other species of mammals as well. For example, vampire bats (*Desmodus rotundus*), which feed on mammalian blood, form roosting groups in which members that have fed successfully sometimes feed regurgitated blood to other group members that have been unsuccessful in foraging. The recipients reciprocate at other times (Wilkinson 1988). Partnerships among individuals are a major feature of many primate societies, and are reinforced by such activities as reciprocal grooming or sexual contact (Figure 16.6).

The theory of reciprocity by partner choice is part of a more general TRANSACTIONAL MODEL OF REPRODUCTIVE SKEW, first developed by Sandra Vehrencamp (1983). The basic idea is that dominant individuals gain from the assistance of subordinate helpers, and "pay" those helpers by allowing them to reproduce just a little more than they could if they left the group and reproduced on their own. Considerable evidence supports this idea (Keller and Reeve 1994, 1999). For example, a dominant dwarf mongoose (a weasel-like African carnivore) suppresses reproduction by older subordinates less than younger subordinates. As subordinates grow older, they are better able to disperse and breed in another group, so the model predicts that dominants should offer them a greater share of the group's reproductive output as an incentive to stay (Creel and Waser 1991). From this perspective, many interactions may be viewed as BIOLOGICAL MARKETS, in which two classes of "traders" exchange "commodities." Market models can be applied to intraspecific cooperation, mutualism between species, and sexual selection (Noë and Hammerstein 1995).

In many situations, cooperation is enhanced if selfish noncooperators are punished: punishment alters the ratio of benefit to cost (Frank 2003). For example, Stuart West and collaborators (2002) have modeled the interaction between legumes (such as beans) and the bacteria—called rhizobia—that invade legume roots, induce formation of an enveloping nodule, and fix nitrogen (N_2) that benefits the plant. The rhizobia obtain photosynthate (carbon) from the plant. This is a potentially unstable interaction, because a rhizobial genotype that cheats, and receives carbon without expending energy on N_2 fixation,

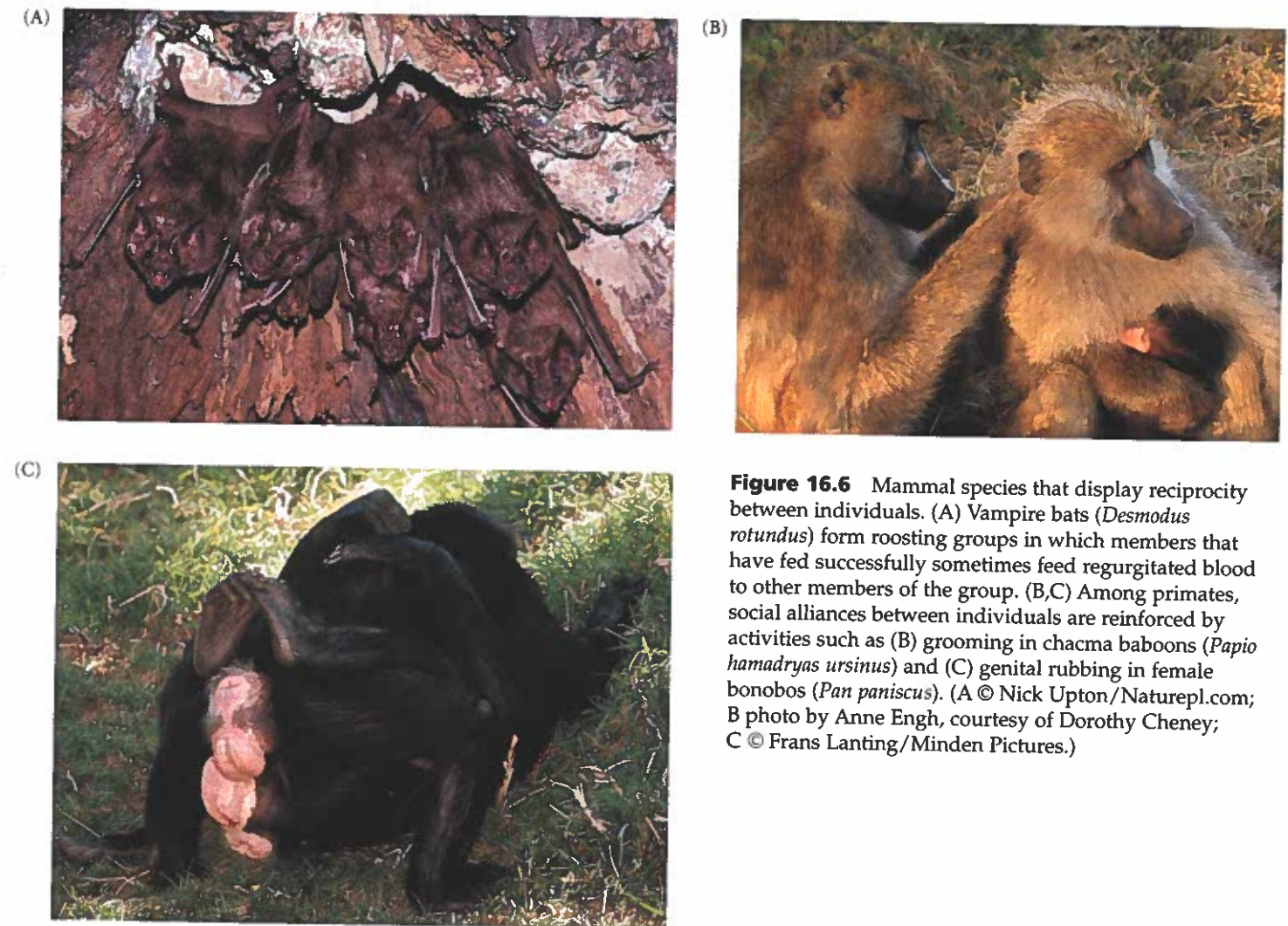
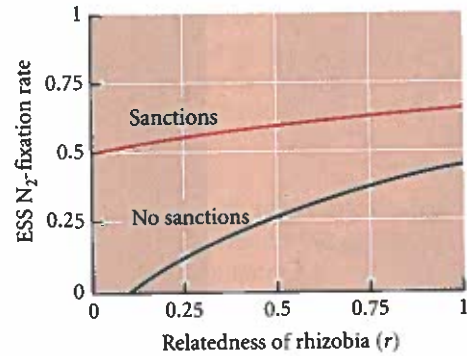


Figure 16.6 Mammal species that display reciprocity between individuals. (A) Vampire bats (*Desmodus rotundus*) form roosting groups in which members that have fed successfully sometimes feed regurgitated blood to other members of the group. (B,C) Among primates, social alliances between individuals are reinforced by activities such as (B) grooming in chacma baboons (*Papio hamadryas ursinus*) and (C) genital rubbing in female bonobos (*Pan paniscus*). (A © Nick Upton/Naturepl.com; B photo by Anne Engh, courtesy of Dorothy Cheney; C © Frans Lanting/Minden Pictures.)

would have an advantage. West et al. showed that the advantage of N_2 fixation depends partly on kin selection (see below), based on a high degree of relationship (r) among bacteria. But the level of N_2 fixation that evolves is greater if the plant preferentially supplies carbon to nodules that fix more N_2 , or punishes nodules that fix less (Figure 16.7). Experiments have shown that legumes do impose such "sanctions" against poorly performing nodules by limiting the supply of oxygen to those nodules (Kiers et al. 2003).

Many interactions are based on "partner choice." Reciprocity can also be favored by "partner fidelity feedback" (Sachs et al. 2004), in which the association between individuals is so long-lasting that the benefits each partner provides to the other feed back to the individual's own benefit. In *The Defiant Ones* (1958), Tony Curtis and Sidney Poitier portray two escaped convicts who, because they are chained to each other, must cooperate even though they dislike each other. When the fitness of each member of a group depends on the fitness of the other members—of the group as a whole—cooperation is clearly in every individual's interest. This principle is important in many biological contexts; perhaps the simplest examples are cooperation among the genes in a cell and among the cells in an organism. If the cell dies, so do all the included genes; if the organism dies, so do its cells. Selection at the higher level—cell or organism—thus eliminates outlaw genes or renegade cells that selfishly diminish the survival of the group. It also favors mechanisms that suppress or destroy such outlaws when they arise. We will see clear examples of this principle later in this chapter.

6.7 A model of the evolutionary nitrogen (N_2) fixation in associated rhizobia. The graph shows an evolutionarily stable strategy (ESS), the relative N_2 fixation that would be the average coefficient of relatedness among rhizobia in a coin-plant were r . The red trace is the same when plant sanctions are modeled (i.e., the plant carbon to a nodule in proportion to the rate of N_2 fixation by rhizobia in that nodule). Plant sanctions increase the ESS level of N_2 fixation. (After West et al. 2002; David McIntyre.)



Root nodules form in the symbiotic relationship between legumes and bacteria of the genus *Rhizobium*.

The evolution of altruism by shared genes

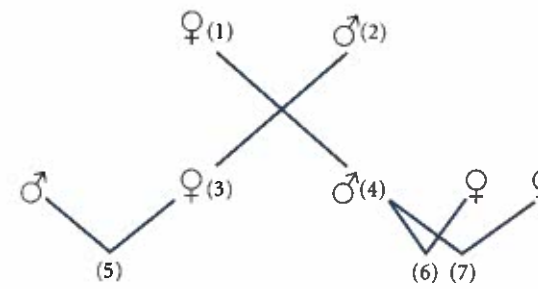
If we think of selection at the level of the gene, we will recognize that an allele replaces another allele in a population if it leaves more copies of itself in successive generations by whatever effect it may have. Commonly, the effect is on the individual organism that carries the allele, but an allele may also leave more copies of itself by enhancing the fitness of other individual organisms that carry copies of that same allele. For instance, an allele for maternal care of offspring increases because it increases the chance of survival of copies of the mother's allele that are carried by her offspring. In a pathbreaking paper, William D. Hamilton (1964) introduced the concept of the **inclusive fitness** of an allele, its effect on both the fitness of the individual bearing it (**DIRECT FITNESS**) and the fitness of other individuals that carry copies of the same allele (**INDIRECT FITNESS**). An individual organism, likewise, has inclusive fitness, with both direct and indirect components. At this level, selection based on inclusive fitness is called **kin selection** because these other individuals are the bearer's relatives, or kin.

Kin selection is one of the most important explanations for cooperation (Hamilton 1964; Michod 1982; Grafen 2006; Lehmann and Keller 2006). Let us suppose that an individual performs an act that benefits another individual, but incurs a cost to itself: a reduction in its own (direct) fitness. The fundamental principle of kin selection is that an allele for such an altruistic trait can increase in frequency only if the number of extra copies of the allele passed on by the altruist's beneficiary (or beneficiaries) to the next generation as a result of the altruistic interaction is greater, on average, than the number of allele copies lost by the altruist. This principle is formalized in **Hamilton's rule**, which states that *an altruistic trait can increase in frequency if the benefit (b) received by the donor's relatives, weighted by their relationship (r) to the donor, exceeds the cost (c) of the trait to the donor's fitness*. That is, altruism spreads if $rb > c$.

The **coefficient of relationship**, r , is the fraction of the donor's genes that are identical by descent to any of the recipient's genes (Grafen 1991). ("Identical by descent" means derived from common ancestral genes, usually within a few previous generations; see Chapter 9.) For example, at an autosomal locus in a diploid species, an offspring inherits one of its mother's two gene copies, so $r = 0.5$ for mother and offspring (Figure 16.8). For two full siblings, $r = 0.5$ also, because the probability is 0.25 that both siblings inherit copies of the same gene from their mother, and likewise from their father.

The simplest example of a trait that has evolved by kin selection is parental care. If females with allele A enhance the survival of their offspring by caring for them, whereas females lacking this allele do not, then if parental care results in more than two extra surviving offspring, A will increase in frequency, even if parental care should cost the mother her life. If $c = 1$ (death of mother) and $b = 1$ (survival of an extra offspring), then since a mother's A allele has a probability of $r = 0.5$ of being carried by her offspring, Hamilton's rule is satisfied by the survival of more than two extra offspring, relative to noncaring mothers.

Interactions among other ("collateral") relatives also follow Hamilton's rule. For instance, the relationship between an individual and her niece or nephew is $r = 0.25$, so



Actor, Recipient	r
Mother (1), offspring (3 or 4)	0.5
Father (2), offspring (3 or 4)	0.5
Full siblings (3, 4)	0.5
Half-siblings (6, 7)	0.25
Aunt (3), niece (6)	0.25
Full cousins (5, 6)	0.125

The coefficient of relationship (r) between actor and the recipient of the action is the average proportion of the actor's genes that are present and identical by descent in the recipient.

Figure 16.8 Coefficients of relationship (r) among some relatives in a diploid species. Individuals 3 and 4 are full siblings, the offspring of female 1 and male 2. Individuals 3 and 4 mate with unrelated individuals, producing offspring 5, 6, and 7. The table gives the values of r between an actor who provides a benefit and the recipient of that benefit.

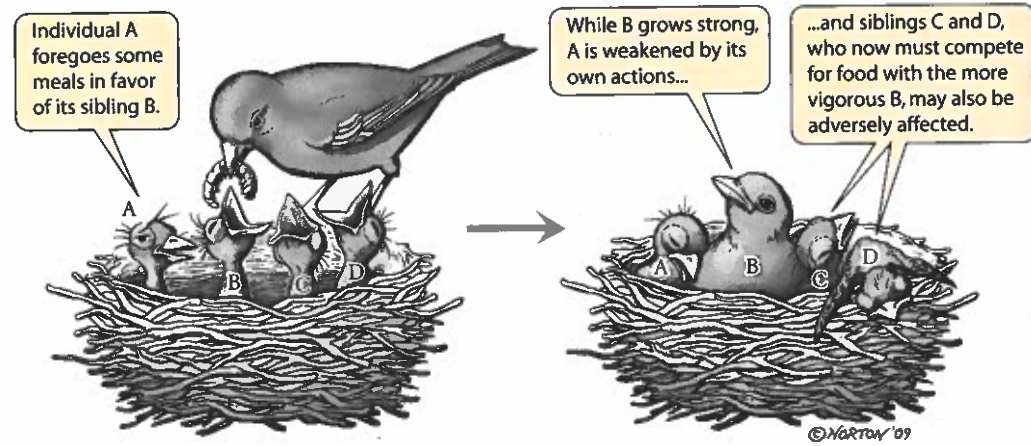
alleles that cause aunts to care for nieces and nephews will spread only if they increase the fitness benefit by more than fourfold the cost of care. The more distantly related the beneficiaries are to the donor, the greater the benefit to them must be for the allele for an altruistic trait to spread.

Parental care illustrates why indiscriminate altruism cannot evolve by individual selection. If allele A caused a female to dispense care to young individuals in the population at random, it could not increase in frequency because, on average, the fitness of all genotypes in the population, whether they carried A or not, would be equally enhanced. Thus the only difference in fitness among genotypes would be the reduction in fitness associated with dispensing care.

Interacting individuals often form groups that last for a generation or less, and that may differ in the frequencies of alleles that determine social behaviors (such as cooperation or defection). David Sloan Wilson (1975) termed these **TRAIT GROUPS**, and proposed that groups with many cooperators may produce more offspring than groups with fewer. When the groups dissolve and random mating takes place before the establishment of new groups, the productive groups of cooperators contribute more genes to the total gene pool, so the allele for cooperation increases in frequency. This process was diagrammed in Figure 15.9, which shows how this process may affect the evolution of sex ratio. Wilson (1997; Wilson and Wilson 2007) has argued that this process vindicates a role for group selection in evolution. Some other authors, however, have pointed out that kin selection can operate only when most interactions are among relatives—in other words, relatives form groups. They argue that trait groups really are made up of individuals that, with respect to genes for cooperation, are more closely related to each other than random. Thus, the view is widely held that kin selection and trait-group selection are two equivalent ways of describing the same process (Frank 1998; Foster et al. 2006; Lehmann and Keller 2006). We return to this point on p. 422.

FACTORS THAT AFFECT THE EFFICACY OF KIN SELECTION. Kin selection can operate only if individuals are more likely to help kin than nonkin. This can be achieved in two ways. First, individuals may be able to distinguish related from unrelated individuals, perhaps based on assessing their similarity with respect to one or more characteristics that are highly variable in the population (Sherman et al. 1997). This variation might be genetically based, or it might be caused by a shared environmental imprint; for example, individual colonies of many ants and other social insects have a distinctive "colony odor" that is apparently derived from food or other environmental factors (Wilson 1971). An example of a kin-selected characteristic, based on kin recognition, is provided by tadpoles of the spadefoot toads *Spea bombifrons* and *S. multiplicata*, which develop into detritus- and plant-feeding omnivores if they eat these materials early in life, or into cannibalistic carnivores, with large horny beaks and large mouth cavities, if they eat animal prey (Pfennig and Frankino 1997). Tadpoles are less likely to develop the cannibalistic phenotype if they develop in the company of full siblings than if they develop alone or in a mixture of related and nonrelated individuals. Moreover, omnivores associate more with their siblings

6.9 Competition among kin can counteract the kin-selected benefits of altruism, which may reduce the fitness of some kin more than it increases the benefit to others. (© John Norton.)



than with nonrelatives, whereas carnivores do the opposite, and carnivores eat siblings much less frequently than unrelated individuals.

Second, kin selection may operate if individuals are usually associated with kin, at least during the period in their life history, or under environmental circumstances, when helping behavior is expressed. Such a population structure requires that individuals have not become randomly mixed before the time of dispersal. For example, local colonies and troops of many primates, prairie dogs, and other mammals are composed largely of relatives (Manno et al. 2007). In such cases, kin recognition would not be necessary. However, aggregation also can increase competition among kin for food and other resources, counteracting kin selection for cooperation because the benefits accrued by recipients of altruistic help are balanced by the reduced fitness of the relatives with which the recipients compete (Figure 16.9; Queller 1994; Frank 1998). Ashleigh Griffin and colleagues (2004) showed experimentally that local competition of this kind can counteract kin selection for cooperation. The bacterium *Pseudomonas aeruginosa* releases compounds called siderophores into the environment to scavenge iron and make it available for bacterial metabolism. This is an altruistic trait because siderophore production is costly, but other individuals can take up siderophore-bound iron and benefit from it. Griffin et al. initiated cultures with mixtures of a siderophore-producing genotype and a cheater genotype, distinguished by color, that does not produce siderophore (Figure 16.10A). Each population consisted of four subpopulations that were combined and mixed at intervals. Relatedness (r) was varied by initiating a culture with either one (high r) or both (low r) of the genotypes. Competition was "global" if the subpopulations were mixed in their entirety, and new subpopulations were then sampled from the mixture; this procedure enabled the productivity of a subpopulation to affect the genetic composition of the entire population. Altruism (siderophore production) might increase a subpopulation's productivity, and so evolve by kin selection. Competition was "local" if the subpopulations contributed equal numbers to the population when mixed; this procedure removes the advantage to a genotype of being in a more productive subpopulation. Over the course of 16 days, the proportion of cooperators (siderophore producers) changed as predicted (Figure 16.10B). In accordance with Hamilton's rule, cooperators increased or stayed at high frequency in the high r treatments but decreased when r was low. But local competition counteracted kin selection, causing the frequency of cooperators to remain unchanged or to decline.

KIN SELECTION OR GROUP SELECTION? In the experiment by Griffin et al., the "global competition" treatment was one in which temporary subpopulations grew to different sizes, based on differences in their genetic composition, and so contributed differentially to the allele frequencies in the pooled population when they were mixed. This conforms precisely to D. S. Wilson's (1975) model of TRAIT-GROUP SELECTION, and suggests that altruism can evolve by group selection, or in general, that multilevel selection (selection at mul-

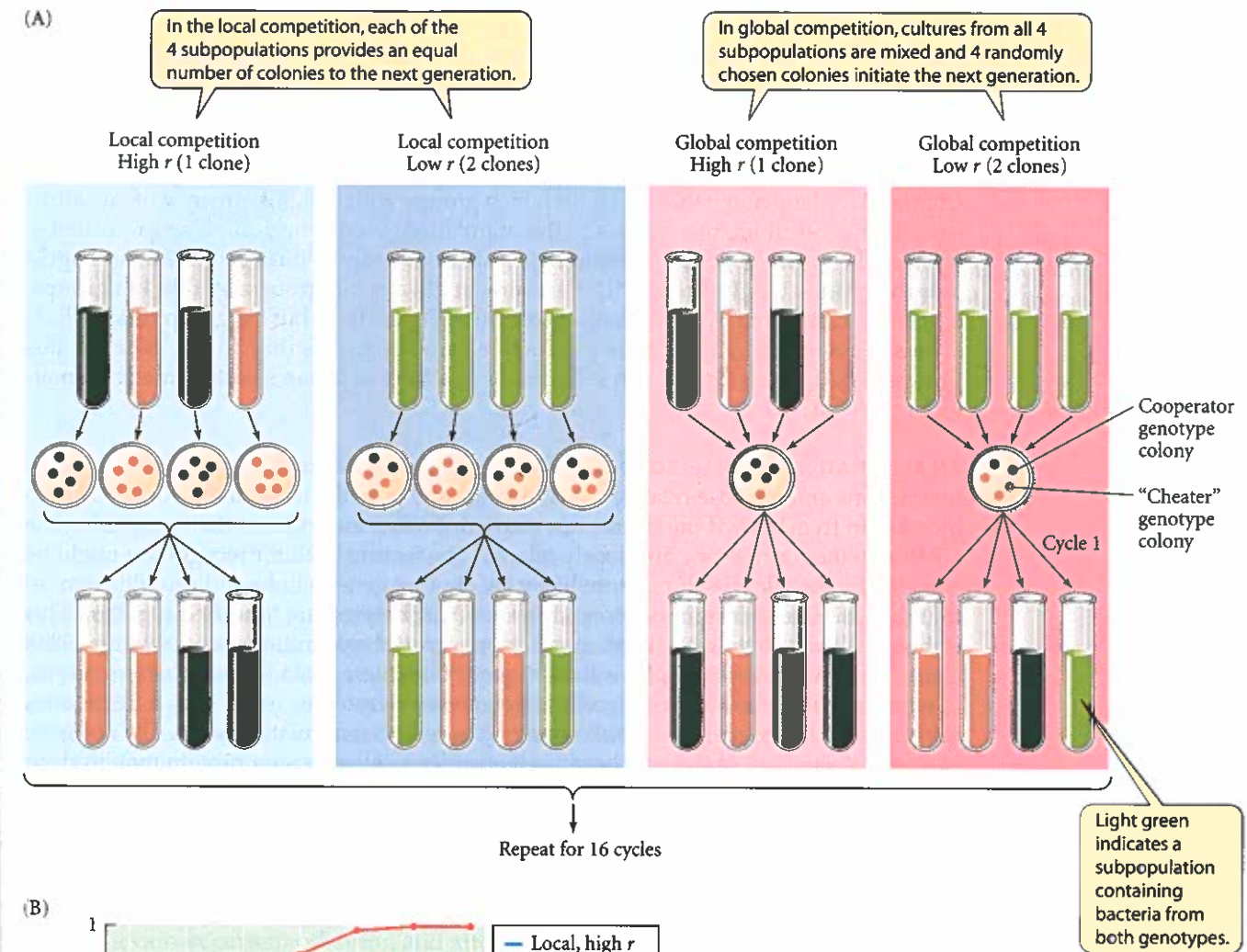


Figure 16.10 An experiment to test the effects of competition and kinship on the evolution of a cooperative trait, siderophore production in the bacteria *Pseudomonas*. (A) Experimental design. Each population consists of four subpopulations, each of which is initiated in every round with either a single clone or with two clones, establishing high versus low relatedness (r). After a period of growth, subpopulations are mixed, and samples from the mixture initiate a new set of subpopulations. (B) Changes in the proportion of the cooperator genotype after 16 cycles, showing that cooperation increases when r is high and competition is global, and decreases when r is low and competition is local. (After Griffin et al. 2004.)

multiple levels, i.e., gene, organism, population) may influence trait evolution. Trait-group selection, however, differs importantly from the kind of group selection that was rejected in the 1960s as too weak to counteract selection at the level of genes or organisms.

It may be useful to recognize two kinds of multilevel selection (MLS), denoted MLS1 and MLS2, which correspond to the two concepts of fitness that were introduced in Chapter 11. The "collectives" and "particles" described in Chapter 11 (see Figure 11.13) are groups and genes, respectively. MLS1 focuses on the frequency of an allele or trait in the entire population, and the groups, or subpopulations, differ in fitness by virtue of how many genes or individuals they contribute to the population (fitness). MLS2 focuses on the numbers of groups that are distinguished by the composition of their genes, and the fitness of groups of a certain type is measured by the number of like groups they pro-

duce (fitness₂). Trait-group selection corresponds to MLS1, whereas group selection of the kind discussed in the 1960s, in which the rate of extinction or proliferation of entire populations determines the prevalence of an altruistic trait, corresponds to MLS2.

Most students of the subject agree that group selection in the shape of MLS2 is unlikely to explain the origin or persistence of an altruistic trait, for the reasons described in Chapter 11. Many agree that MLS1, in which groups with a high frequency of an “altruistic allele” contribute more genes to the population-wide gene pool, is an important—perhaps the most important—way in which altruism evolves. But most researchers agree that the groups that figure in MLS1 are almost always kin groups. Within kin groups, altruism is disfavored by individual selection (see Figure 16.9), but kin groups that include altruistic genotypes may be more productive than kin groups that do not. Whether this process is better described as kin selection or as a form of group selection may be a matter of preference.

AN ALTERNATIVE TO KIN SELECTION. Although altruism is thought usually to evolve by interactions among close relatives, it is theoretically possible for an allele for altruism to increase in frequency if the bearer can recognize other individuals that carry the same allele, whether or not they are closely related. The feature used for recognition might be encoded by the allele itself or, more likely, by another gene in linkage disequilibrium, so that the trait used for recognition and the gene for helping are inherited together. This is the so-called GREEN BEARD MODEL, named for a fanciful recognition trait (Dawkins 1989). One of the few known examples is the *csA* gene of the slime mold *Dictyostelium discoideum*, in which (as described on p. 415) cells aggregate into a moving “slug” that differentiates into reproductive spores and a stalk made up of cells that altruistically die. The *csA* gene promotes formation of the slug because it encodes a cell adhesion protein that binds to the protein in the membrane of other cells. When David Queller and collaborators (2003) mixed wild-type cells and cells in which *csA* was knocked out, the knockout cells were excluded from the slug, and so few of them became spores. Wild-type *csA* genes promote their own reproduction by forming colonies of cells in which some *csA*-bearers sacrifice themselves for the reproductive benefit of others.

A Genetic Battleground: The Family

At first surmise, it would seem that relationships within families should be the epitome of cooperation, since the parents' fitness depends on producing surviving offspring. However, evolutionary biologists have come to understand that these interactions are pervaded with potential conflict, and that much of the diversity of reproductive behavior and life histories among organisms stems from the balance between conflict and cooperation. (Incidentally, the ways in which some animal species behave toward family members starkly show that natural selection utterly lacks morality, as pointed out in Chapter 11.)

Mating systems and parental care

Whether or not one or both parents care for offspring varies greatly among animal species and partly determines the MATING SYSTEM, the pattern of how many mates individuals have and whether or not they form pair-bonds (Clutton-Brock 1991; Davies 1991). Providing care (such as guarding eggs against predators, or feeding offspring) increases offspring survival, which enhances the fitness of both parents (and of the offspring). But parental care is also likely to have a cost. It entails risk, and it requires the expenditure of time and energy that the parent might instead allocate to further reproduction: a female might lay more eggs, and a male might find more mates.

In most animals, neither parent provides care to the eggs or offspring after eggs are laid, and one or both sexes, especially in long-lived species, may mate with multiple partners (PROMISCUOUS MATING). In many birds and mammals, females provide care but males do not, and males may mate with multiple females (POLYGYNY). In some fishes and frogs and a few species of birds, only males guard eggs or care for offspring, and in some such species, the female may mate and lay eggs with different males (POLYANDRY). (These terms stem from

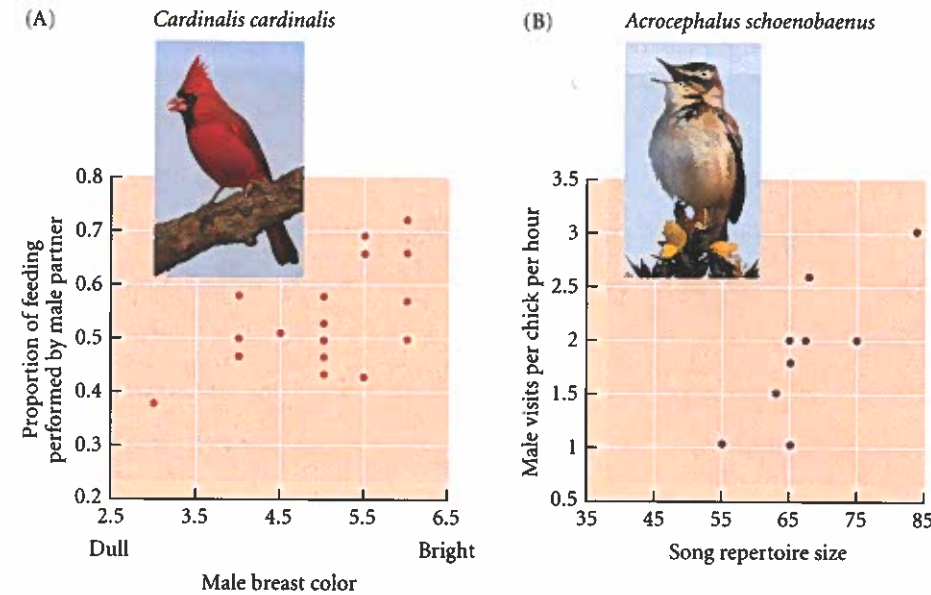


Figure 16.11 Examples of variation in paternal care correlated with signal traits in songbirds. (A) Paternal care is correlated with the brightness of the male's breast in the northern cardinal. (B) Among sedge warblers, males that sing a larger repertoire of songs also bring food to offspring more frequently. (A after Linville et al. 1998, photo © Purestock/Alamy; B after Buchanan and Catchpole 2000, photo © Mark Hicken/Alamy.)

the Greek *polys*, “many”; *gyne*, “woman”; *andros*, “man.”) In many species of birds, some mammals, and a few insects such as dung beetles, a female and male form a “socially monogamous” pair-bond and contribute biparental care of the offspring. However, many such birds engage in frequent “extra-pair copulation” and are not sexually monogamous. As we have seen, females may also increase their reproductive success by laying eggs in the nests of unwitting foster parents. Females in some pair-bonding species of birds appear to favor males with characteristics that serve as honest signals of paternal caregiving (Figure 16.11). This is as some theory predicts (Kokko 1998), but it has also been argued that highly ornamented males might devote less time to offspring care and more to extra-pair copulation, in which they may be especially likely to succeed (Houston et al. 2005).

Each parent in a mated pair will maximize her or his fitness by some combination of investing care in current offspring and attempting to produce still more offspring. In a species with biparental care, each parent would profit by leaving as much care as possible to the other partner, as long as any resulting loss of her (or his) fitness owing to the death of her (or his) current offspring were more than compensated by the offspring she (or he) would have from additional matings. If offspring survival were almost as great with uniparental care as with biparental care, selection would favor females that defected, abandoning the brood to the care of the male—or vice versa (Figure 16.12). Thus a conflict between mates arises as to which will evolve a promiscuous habit and which will

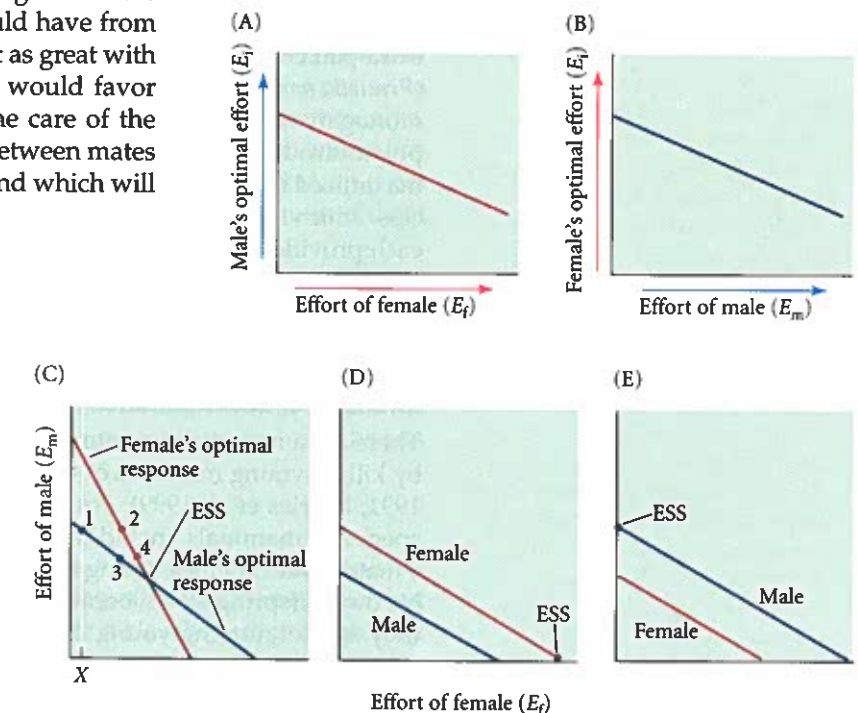


Figure 16.12 An ESS model of parental care. (A,B) The optimal parental effort expended by each sex declines, the more effort its partner expends. (C) Curves for males and females plotted together. Their intersection marks the ESS, the evolutionarily stable strategy. If, for example, the population starts with female effort (E_f) equal to X , male effort (E_m) evolves to point 1; but then the optimal E_f is at point 2 on the female's optimality line. When E_f evolves to point 2, E_m evolves to point 3; but then E_f evolves to point 4. Eventually, E_m and E_f evolve to the intersection (the ESS), no matter what the initial conditions are. (D,E) Conditions can be envisioned in which the optimal curves for the sexes do not intersect and the ESS is care by only the female (D) or the male (E). (After Clutton-Brock and Godfray 1991.)